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Shane R. Siers
Colorado State University, shane.r.siers@aphis.usda.gov

Julie A. Savidge
Colorado State University, julie.savidge@colostate.edu

Robert N. Reed
USGS Fort Collins Science Center, reedr@usgs.gov

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Research Article

Ontogenetic and ecological variation in invasion risk of Brown Treesnakes (*Boiga irregularis*) on Guam

Shane R. Siers[1,2,*], Julie A. Savidge[1] and Robert N. Reed[3]

[1]*Colorado State University, Department of Fish, Wildlife and Conservation Biology, Fort Collins, Colorado 80523, USA*
[2]*Current address: USDA/APHIS/Wildlife Services, National Wildlife Research Center, P.O. Box 10880, Hilo, HI 96721, USA*
[3]*U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado 80526, USA*

Author e-mails: shane.r.siers@aphis.usda.gov (SS), julie.savidge@colostate.edu (JS), reedr@usgs.gov (RR)

**Corresponding author*

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Abstract

Size structure within populations of invasive species may have consequences for relative risk at all stages of the invasion process, with implications for management interventions such as interdiction, suppression, and eradication. To assess relative distributions of invasive Brown Treesnakes (*Boiga irregularis*) among demographic categories of management interest, we undertook the most comprehensive and controlled sampling in > 25 years of research into this ecologically and economically destructive introduced predator. We collected a seasonally-balanced sample of 100 snakes from each of 18 sites, stratified by six habitat types, encompassing the species' entire extralimital range. Samples indicated significant differences in distributions of female and male snakes among management classes (juvenile, transitional, and mature) by site and habitat. We found substantial heterogeneity in localized population characteristics over relatively small geographic distances, only modest influence of habitat type, higher prevalence of reproductively mature snakes in savanna and urban habitats, and an alarmingly high proportion of snakes that are too small to be effectively targeted by current rodent-baited control tools (mean = 38.2%, range = 19 to 72%). Failure to account for such variability in high risk demographic fractions may hinder successful interventions.

Key words: demographic heterogeneity, invasion process, landscape-scale suppression, management risk, population ecology

Introduction

Life history stages of invasive species may exhibit differences in relative risks and challenges associated with their management (Sakai et al. 2001). Proportions of individuals in each life history stage may vary throughout the organism's range due to population dynamics and local ecological characteristics. Accounting for variability in population characteristics associated with local ecological differences may help optimize plans for management.

The invasion of Guam by the Brown Treesnake (*Boiga irregularis* Merrem, 1802) serves as a stark example of ecological and economic devastation wrought by an introduced predator, particularly in vulnerable island ecosystems (Savidge 1987; Fritts and Rodda 1998; Rodda and Savidge 2007). Management interventions have primarily focused on preventing spread of this predator to other vulnerable Pacific islands such as the Commonwealth of the Northern Mariana Islands and the state of Hawaii. Beyond interdiction, management objectives for Brown Treesnake populations on Guam include suppression of snake numbers, leading to the recovery of key habitat for reintroduction of native wildlife and reduction or elimination of other impacts on Guam's economy, ecology, and society (U.S. Fish and Wildlife Service 2009). Landscape-scale suppression of Brown Treesnakes on Guam has been demonstrated to be feasible through the aerial application of toxic baits over forest habitat (Dorr et al. 2016; USDA unpublished data). However, little is known about how population characteristics of Brown Treesnakes vary across Guam's landscape.

Figure 1. Snakes of different sizes pose different invasion and management risks. In this image, the 450-mm juvenile snake is less susceptible to rodent-baited control tools and more likely to be accidentally transported in cargo. The mature 1250-mm snake is more likely to prey on larger native prey species and poses more risk of establishing a new population by reproduction. Photo by Shane R. Siers.

To inform plans for landscape-level suppression, we sought to characterize how Brown Treesnake populations vary in demographic fractions associated with elevated management risk across the range of habitat characteristics on Guam.

We assert that the two most important individual characteristics associated with Brown Treesnake demography are body size and sex. From hatching to full maturity, a Brown Treesnake may undergo a six- to seven-fold increase in body length and a 400-fold increase in body mass (Figure 1) (Siers 2015). These changes can have marked consequences for nearly all aspects of an individual's natural history throughout its ontogeny, including locomotion, thermoregulation, microhabitat use, predation, optimum prey size, and vulnerability to control technologies.

Management risks and challenges associated with size class and sex vary based upon which stage of the invasion process is being considered (Table 1). Smaller snakes are limited to small prey and rarely forage or move terrestrially (Rodda and Reed 2007). However, smaller snakes are more likely to be accidentally transported (Vice and Vice 2004), and may be less likely to be promptly discovered or reported if transported to a novel environment. Larger snakes can take a wider variety of prey items, including larger native fauna and domestic animals (Savidge 1988), and are more inclined to forage terrestrially (Rodda and Reed 2007); the latter may lead to more movement among fragments within habitat types and movements among habitat types such as into savanna and urban habitats where larger snakes are more often observed (Savidge 1991). Brown Treesnakes are averse to crossing roads (Siers et al. 2014), but larger snakes are more likely to cross forest gaps and roads than smaller snakes (Siers et al. 2016). Larger snakes are also more likely to inflict medically significant bites to infant humans (Fritts et al. 1990; Fritts and McCoid 1999). Males attain larger body size than females (Savidge 1991) and can presumably prey on a wider size distribution of native and domestic fauna. Mature females (particularly gravid or sperm-storing females) pose the highest risk of new population establishment after accidental transportation to a snake-free island.

Brown Treesnakes show a distinct ontogenetic shift from ectothermic to endothermic prey (Savidge 1988; Greene 1989; Mackessy et al. 2006), with smaller size classes of snakes feeding exclusively on small lizards (Savidge 1988; Siers 2015). Thus, rodent-baited control methods such as traps (Rodda et al. 1999a) or toxicant-laden baits (Savarie et al. 2001; Lardner et al. 2013) are largely ineffective against snakes < 700 mm snout-vent length (SVL) and partially effective against snakes from 700–900 mm (Rodda et al. 2007). However, larger snakes, which are attracted to mammalian prey, are susceptible to these methods. While carrion-baited traps capture snakes smaller, on average, than those baited with live mice (Shivik and Clark 1999), the mean size of snakes captured with carrion baits was within the size range for which we consider rodent baits to be partially

Table 1. Ontogenetic shift in invasion risk by management classification throughout the invasion process. Juvenile = both sexes < 700 mm SVL; transitional = 700 to 1025 mm (females) or 1030 mm (males); mature = females > 1025 mm and males > 1030 mm

Invasion Stage	Juvenile Risk	Transitional Risk	Mature Risk
TRANSPORT: Risk of being moved to a new location	HIGHER: Small snakes more often found in outbound cargo.[a] Invulnerable to port protection traps and toxicant baits that filter out larger snakes[b]	MODERATE: Most numerous size class of snakes (Figure 3) but relatively susceptible to interdiction tools	LOWER/HIGHER: Adult snakes more likely to be trapped before reaching cargo or detected by cargo inspectors; however, larger snakes more likely to cross roads[c] such as typically surround ports of exit
ESTABLISHMENT: Risk of founding a new population upon being transported	LOWER: Very small snakes are not yet reproductively mature,[d] may experience higher mortality before maturation	MODERATE: Contains some reproductive individuals, with non-reproductive snakes approaching maturation	HIGHEST: Reproductively mature females have highest per capita reproductive potential. A single gravid female may establish a new population. Males may pose only moderate risk, with per capita risk decreasing at higher densities as mature females become the rate-limiting stratum
DETECTION LAG: Risk of not being observed or not prompting reaction in new location	HIGHER: Smaller size classes are harder to detect[b] and less likely to leave arboreal habitats,[e] thus less likely to be observed by the public and reported	MODERATE: Relatively more observable, more likely to be reported to a management agency	LOWEST: More likely to be found in urban habitats,[f,g,h] more likely to be noticed (e.g. while crossing roads[c]) and reported, particularly very large males
SPREAD: Risk of moving from introduction site to new location	LOWER: Very small snakes appear to move less, particularly across terrestrial gaps, e.g., roads[e,h]	MODERATE: More vagile than smaller snakes	HIGHER: More likely to move longer distances, more likely to forage away from forest habitat,[g,h] more likely to cross roads.[c] May form the invasion front, spreading as local supplies of large prey are depleted[i,j]
IMPACT: Risk of ecological or economic damage associated with invasion	LOWER: Prey only on small lizards, low per capita impact. Too small to pose any risk to humans or domestic animals. Impact only higher with high densities on sensitive prey species[k]	MODERATE: Wider range of prey take, e.g., eggs of smaller birds[f]. Most abundant size range, with impact increasing with density	HIGHEST: Larger snakes take a much wider range of prey sizes, including native threatened and endangered fauna[f] and domestic animals,[l] and inflict bites on humans[m] and human infants,[n] particularly male snakes that achieve much greater sizes
CONTROL: Risk of evading effective targeting by interdiction or suppression tools	HIGHEST: Almost completely impervious to rodent baits, used in all major control tools[b,o,p]	MODERATE: Increasingly trappable with size, rodent baits nearly fully effective by 900 mm SVL[b]	LOWER/HIGHER: Rodent baits fully effective; however, any failure to effectively target gravid females poses high risk of control failure due to perpetuation of reproduction. To the extent that roads and forest gaps form barriers to snake movement[q] and may be used as boundaries for management units, larger snakes are more likely to cross those boundaries[c]

Citations: [a]Vice and Vice 2004; [b]Rodda et al. 2007; [c]Siers et al. 2016; [d]Savidge et al. 2007; [e]Rodda and Reed 2007; [f]Savidge 1988; [g]Savidge 1991; [h]Siers 2015; [i]Savidge 1987; [j]Rodda et al. 2008; [k]Rodda and Fritts 1992b; [l]Fritts and McCoid 1991; [m]Fritts and McCoid 1999; [n]Fritts et al. 1990; [o]Lardner et al. 2009a; [p]Lardner et al. 2013; [q]Siers et al. 2014

effective, and subsequent work has demonstrated that dead neonatal mouse baits are not effective for the smallest size classes of Brown Treesnakes (Lardner et al. 2009a; Lardner et al. 2013).

The objectives of this study were to assess distributions of Brown Treesnake size classes in different habitats across the Guam landscape and relate our findings to implications for interdiction and suppression. To achieve these aims, we established a comprehensive, habitat-stratified sampling protocol spanning the island of Guam, the entire known extralimital range of this species.

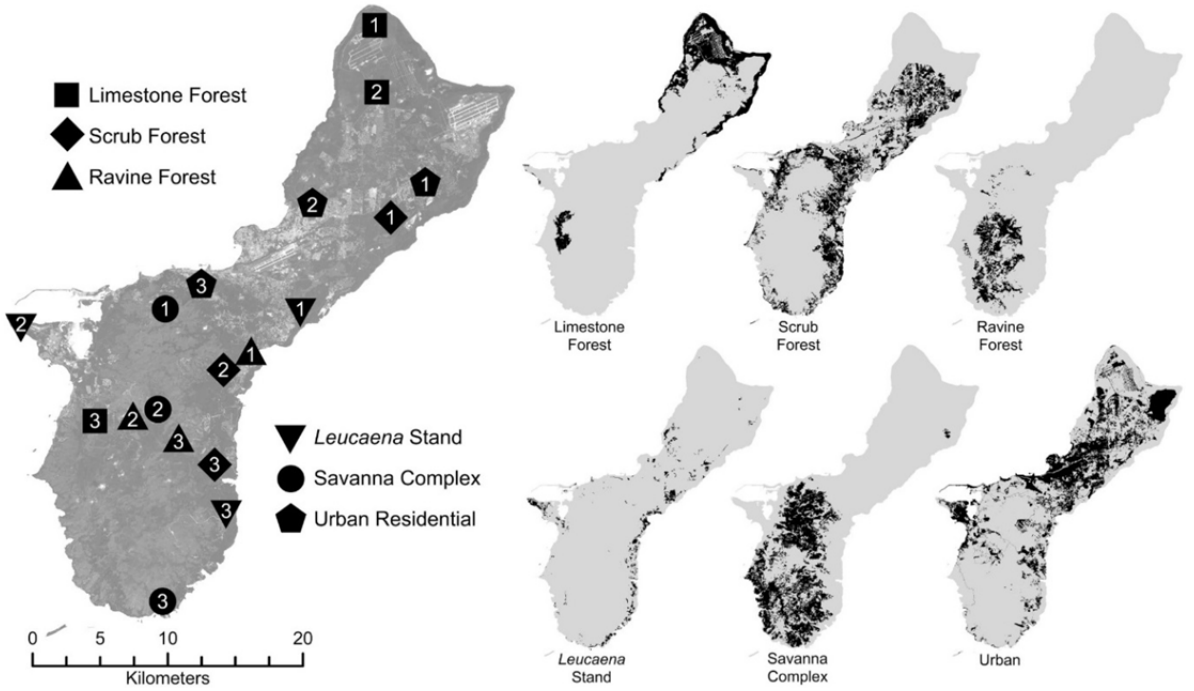

Figure 2. Habitat classification map of Guam depicting the distribution of the six target habitat types (Liu and Fischer 2005) and 18 sample locations. Symbols represent habitat types and numbers refer to the respective replicate (1–3) within each habitat type.

Methods

Habitat stratification and site selection

We selected three study sites within each of six habitat types as classified by Liu and Fischer (2005) following the nomenclature of Mueller-Dombois and Fosberg (1998). Sites were dispersed across Guam and contained large uninterrupted tracts representative of the respective habitat types. Limestone forest (LIM; 13% of Guam's land cover) is characterized by moist, broadleaved evergreen forest of predominantly native species on elevated limestone plateaus. These habitats are critical to the preservation and recovery of Guam's native flora and fauna (U.S. Fish and Wildlife Service 2009). Ravine forests (RAV; 8%) are low-lying areas bordering flowing and ephemeral rivers, and are primarily moist green forests containing higher proportions of palms, bamboos, and *Pandanus*. Scrub forest (SCR) is variable and comprised primarily of secondary growth of non-native species on disturbed land. It is the most extensive class of forest on Guam, covering 23% of Guam's land mass and comprising 58% of forest cover. *Leucaena* stands (LEU; 3%) are primarily comprised of *Leucaena leucocephala* ("Tangantangan"), an introduced species often used in many parts of the world to revegetate deforested areas. *Leucaena* provides excellent habitat for several introduced species, including Brown Treesnakes (Rodda et al. 2001). Nearly all forests on Guam have some amount of *Leucaena*, particularly along edges; however, in some areas it forms nearly monotypic stands. Savanna complex (SAV; 21%) is characterized by a mosaic of grassland interspersed with emergent shrubby vegetation and erosion scars, and comprises a significant proportion of Guam's southern region. While we presume densities of this arboreal snake are lower in savanna than in forest habitat, they are abundant in this habitat and savanna snakes will require consideration in any landscape-level suppression or eradication effort. Urban areas (URB; 27%) are diverse and include industrial, commercial, and residential areas. For reasons of consistency, access, and to increase public awareness, we elected to concentrate our surveys in and around urban residential areas. These six habitat types comprise 95% of Guam's land cover (Figure 2).

Survey methods

We conducted visual surveys to sample snake populations at the 18 selected sites. We commenced surveys at sunset and searched for snakes for three to four hours, overlapping much of the peak activity

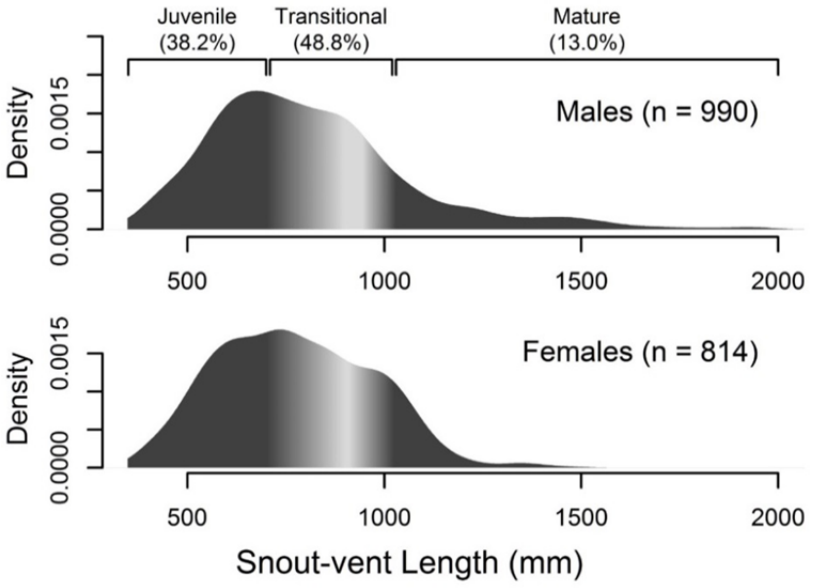

Figure 3. Size distributions of male and female snakes sampled at all 18 sites. Note the longer right tail for larger male snakes. Shadings in the "transitional" class represent the shifts toward trapping susceptibility at the lower margin and maturity at the upper margin.

period of Brown Treesnakes (Rodda et al. 1999b). Trained searchers were equipped with powerful headlamps with beam characteristics that optimize detection (Lardner et al. 2009b). Searchers followed habitat edges at a slow pace, roughly 0.5 km per hour, examining visible vegetation and non-vegetative structure for presence of snakes. We surveyed forest habitats mainly from road edges. Savanna searches included road edges, footpaths, and trackless searches throughout the habitat mosaic, including edges of erosion scars. We conducted urban surveys by searching structures and vegetation in residential yards; all yards were separated from large forest tracts by at least one paved road. Searchers stopped searching when encountering habitat formations inconsistent with search objectives (e.g., clearings in forest habitat or large stands of trees in urban habitat) and resumed searching upon returning to representative habitat.

Visual survey provides low yield per unit effort, but samples that are more representative of the population and with less size bias when compared to trapping (Rodda et al. 2007), and is the only survey method demonstrated to sample all size classes of snakes (Rodda and Fritts 1992a). In a capture-mark-recapture study in a geographically closed population of Brown Treesnakes in limestone and secondary forest habitat (Christy et al. 2010), visual surveys under-represented the smallest and largest snakes; therefore, relative abundances among size classes represent populations as sampled by visual searches rather than known relative abundances. This bias toward mid-sized snakes should be kept in mind when interpreting size distributions within populations (e.g., Figure 3). Because our primary intent was to examine differences in size class distributions among habitats, rather than among populations, we consider the comparisons to be valid. To date there have been no assessments of differences in size class detectability among habitat types, a source of potential error in interpreting these results.

Sampling objectives

To obtain enough data to accurately describe size distributions, we selected a target sample of 100 snakes from each of the 18 sites. To minimize biases resulting from short-term population dynamics or seasonal effects, we balanced sample sizes between the wet season and dry season, with at least two quarterly bouts per season (one sampling period in the first half of the season and another in the last half). The one exception to this sampling scheme was the second limestone forest replicate (LIM2), which was sampled in one relatively continuous effort due to impending closure of a snake-proof barrier; 90 snakes were collected at this site in the wet season and 10 in the dry season.

Seasons were delineated by calendar dates based on historic rainfall records for Guam (wet = June through November, dry = December through May) rather than actual weather conditions at the time of sampling. While this may mask short-term weather trends that may have influenced our samples, we intended to minimize such weather effects by sampling over multiple bouts during seasons.

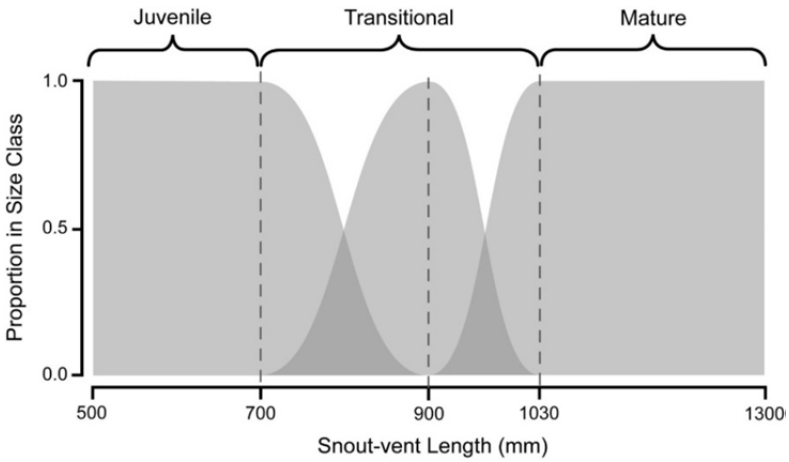

Figure 4. Idealized representation of the transition from juveniles, which are refractory to rodent-based control tools, to intermediately-targetable but immature "transitional" snakes, then to mature snakes that are vulnerable to rodent-based control tools. Maturation sizes vary slightly for males and females, as discussed in the text (Savidge et al. 2007).

Snake processing

Upon visual detection, snakes were hand-captured. Surveyors recorded time and location, and morphometric data including snout-vent length (SVL, obtained by stretching the snake along a flexible tape ruler), and weight (using Pesola spring scales; Pesola AG, Baar, Switzerland). Captured snakes were transported to the U.S. Geological Survey Brown Treesnake Lab the following morning, where SVL and weight were re-measured to validate field data. Snakes were then euthanized and necropsied. We determined sex by examining internal reproductive anatomy.

Management classification

Reproductive status of Brown Treesnakes is most practically estimated by SVL benchmarks established by Savidge et al. (2007), who found that 95% of female snakes matured between lengths of 910 and 1025 mm, while males matured from 940 to 1030 mm. Based on size and sex characteristics and associated differences in management risk, we designate three management classes for invasive Brown Treesnakes: 1) "juvenile," snakes of both sexes measuring under 700 mm SVL, which are refractory to rodent-based attractants and baits and completely sexually immature; 2) "transitional," snakes from 700 mm to 1025 mm (females) or 1030 mm (males), of intermediate attraction to rodents and sexual maturity; and 3) "mature" snakes, fully vulnerable to rodent-based attractants and baits, with subclassifications of "mature males" (with greater possible impacts due to larger size potential) and "mature females" (with greater reproductive potential) (Figure 4). We depicted distributions of snakes among management classes by site and habitat groupings in a box plot. Differences in distributions among classes were tested by comparing observed counts within management categories to those expected by pooling all other sampled sites as a reference distribution using Fisher's exact test. Separate Chi-square tests were used to assess significant deviation from 1:1 sex ratios and differences in the proportion of the sample that were mature females.

We assessed regional similarities in proportions within management classifications by hierarchical clustering (average method based on a correlation distance matrix) using the R package "pvclust" (Suzuki and Shimodaira 2015), which produces a clustering dendrogram with approximately unbiased *p*-values for clusters via multiscale parametric bootstrap resampling. We plotted cluster nodes on a map to visually assess relative geographic aggregation or non-aggregation of sites within clusters.

Site-level and habitat-level heterogeneity in prevalence of 1) attractant-refractory juveniles of both sexes, 2) high-impact mature males, and 3) mature females of high establishment risk were independently tested by assessing fit of models describing alternative hypotheses associated with various site identity and habitat classification schema using logistic regression. The binary response variable was whether a given snake did or did not belong to the management class of interest. The term *site* assigned a categorical covariate for each of the 18 sites, allowing full site-by-site variability in estimation of prevalence—or, proportion of population—for each of the response variables (management classes). The alternate classification *hab* pooled all sampled snakes into one of six nominal habitat types (limestone forest, scrub forest, ravine forest, *Leucaena* stand, savanna complex, and urban residential) to assess whether prevalence varied by habitat type. Other alternatives included *fsu* which lumped four forest

Table 2. Search areas (minimum convex hull areas around search locations), minimum and maximum dimensions, and survey dates, by season, for visual survey sampling. Note that search areas often had complex geometries; hulls often included un-representative habitat that was not searched and often bordered on much larger tracts of representative habitat.

Site	Convex hull area (ha)	Min/max dimension (m)	Survey dates (dry season)	Survey dates (wet season)
LIM1	168.7	1480 – 1975	22 Mar 2010 – 27 May 2010 20 Dec 2010 – 21 Dec 2010	7 Jun 2010 – 8 Nov 2010
LIM2	57.7	485 – 1290	18 May 2010	1 Sep 2010 – 28 Oct 2010
LIM3	47.2	562 – 1595	6 Jan 2011 – 19 Apr 2011	21 Jun 2011 – 13 Oct 2011
SCR1	181.2	1300 – 1710	3 Jan 2011 – 3 May 2011	13 Jul 2010 – 3 Nov 2010; 9 Nov 2011
SCR2	15.7	310 – 920	16 May 2011 – 26 May 2011 5 Dec 2011 – 3 Jan 2012	31 Aug 2011 – 25 Oct 2011 7 Jun 2012 – 13 Aug 2012
SCR3	28.7	416 – 1151	18 May 2011 – 31 May 2011 1 Dec 2011 – 25 Jan 2012	17 Aug 2011 – 1 Nov 2011 6 Jun 2012 – 2 Jul 2012
RAV1	14.9	369 – 734	1 Dec 2011 – 12 Apr 2011	19 Oct 2011 – 8 Nov 2011 5 Jun 2012 – 20 Aug 2012
RAV2	22.7	513 – 728	5 Jan 2011 – 20 Apr 2011	23 Jun 2011 – 24 Oct 2011
RAV3	19.4	356 – 775	5 Dec 2011 – 22 Mar 2012	4 Aug 2011 – 8 Nov 2011 6 Jun 2012 – 6 Aug 2012
LEU1	36.8	612 – 1112	10 Feb 2011 – 31 May 2011	6 Jun 2011 – 26 Sep 2011
LEU2	58.5	684 – 1540	15 Feb 2011 – 25 Apr 2011	20 Jun 2011 – 27 Sep 2011
LEU3	2.2	30 – 845	25 Jan 2011 – 10 May 2011	11 Aug 2011 – 31 Oct 2011 7 Jun 2012 – 7 Aug 2012
SAV1	71.2	437 – 2205	14 Apr 2011 – 23 May 2011	28 Jul 2011 – 29 Nov 2011
SAV2	13.3	161 – 1330	20 May 2010 27 Dec 2010 – 5 May 2011	22 Nov 2010 – 23 Nov 2010 13 Jun 2011 – 17 Nov 2011
SAV3	40.5	365 – 1536	4 Jan 2011 – 7 Apr 2011	20 Jul 2011 – 8 Nov 2011 4 Jun 2011 – 15 Aug 2011
URB1	12.5	301 – 635	13 Dec 2011 – 8 May 2012	4 Jun 2012 – 27 Sep 2012
URB2	27.2	409 – 937	20 Dec 2011 – 1 May 2012	4 Jun 2012 – 20 Sep 2012
URB3	44.4	704 – 966	15 Dec 2011 – 17 Apr 2012	5 Jun 2012 – 13 Sep 2012

types (limestone, scrub, ravine, and *Leucaena*) into one forest classification and left savanna and urban habitats to vary independently (three habitat classes), and *frsu* which pooled limestone, scrub and *Leucaena* forests, but allowed ravine forest to vary independently along with savanna and urban habitats, based on a priori observations of field observers that ravine forest searches tended to produce lower rates of snake captures than in other forest habitats and snakes that were in poorer body condition (four classifications). Additionally, as we balanced sampling between wet and dry seasons, the term *seas* was investigated for additive and interactive effects of season on prevalence of snakes in respective management classes. The higher-order or "global" model for this assessment was:

$$logit(\pi) = \beta 0 + \beta[class] + \beta seas + \beta[class] * seas$$

where π is the estimated proportion, or prevalence, of the respective management class, and [*class*] is one of the four habitat classification alternatives (*site*, *hab*, *fsu* or *frsu*). All possible nested combinations of terms were considered, resulting in a set of 14 candidate models, including season-only and intercept-only (single prevalence estimate) models. We conducted logistic regression using R version 3.0.2 base function "glm" (family = "binomial"; R Core Team 2013). Model selection was based upon an information-theoretic approach (Akaike's Information Criteria corrected for small sample size, AIC_c).

Results

Sampling occurred from 22 March 2010 to 27 September 2012. The extent of search areas and sampling dates, by season, are listed in Table 2. The minimum convex hull areas for each survey site ranged from 2.2 to 181.2 ha; however, search area geometries were highly variable – not all habitat within these areas was representative of the target habitat type and hulls often bordered on much larger tracts representative of the same habitat. For example, the smallest survey area of 2.2 ha, LEU3, was along a straight road segment bisecting a large (> 30 ha) tract of continuous *Leucaena* habitat; while the minimum dimension of the search area (the road edges) was only approximately 30 m, the length of the searched area extended over 845 m.

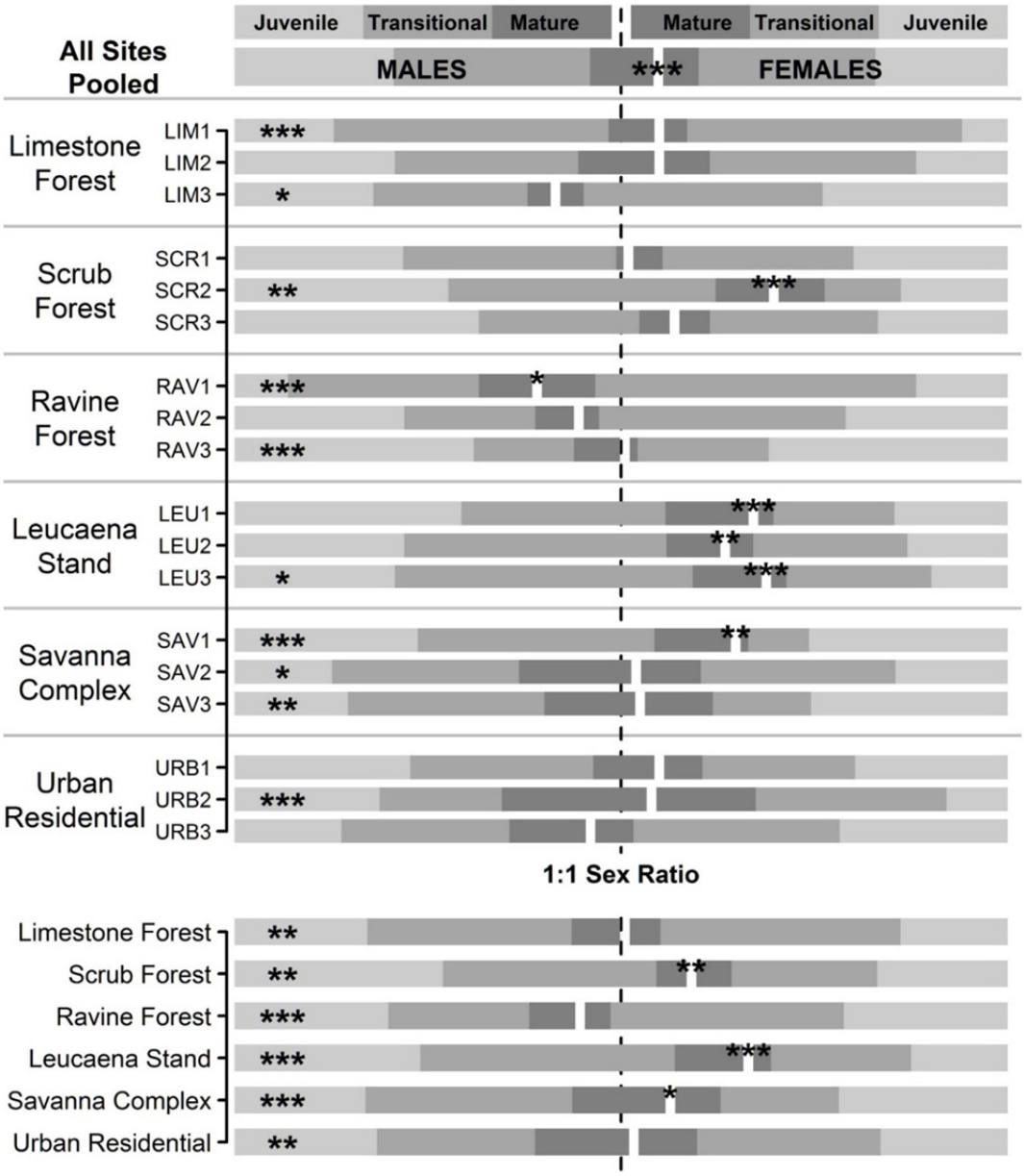

Figure 5. Breakdown of site samples by proportions of Brown Treesnakes in management classes, with the bottom six bars representing pooling of sites by habitat type. Asterisks on bars at left indicate significance of differences from the distribution of all other sites combined, excluding the one tested. The vertical dashed line indicates a 1:1 sex ratio, and asterisks between the bars of sexes indicate a significant sex bias. P-values: "*"<0.05, "**"<0.01, "***"<0.001.

We captured a mean of 100 snakes (n = 99 to 104) at each of the 18 study sites, for a total of 1804 snakes (990 males and 814 females). Juvenile snakes (< 700 mm) constituted 38.2% of the sample, transitional snakes accounted for 48.8%, and the remaining 13.0% (8.3% males, 4.7% females) were classified as mature per size criteria of Savidge et al. (2007). Qualitatively, size distributions in Figure 3 depict a concentration of snakes in the 500 to 1000 mm size range with a long right tail in larger size classes, particularly for males.

The distribution of sampled snakes among different management classes varied significantly within and among habitat types (Figure 5). Overall, most sites yielded a large proportion of transitional snakes with considerable variability among sites in proportions of

juvenile and mature snakes. Ten of 18 sites exhibited significant variation when compared to all other sites pooled, including all three savanna sites. When samples were pooled by habitat type, all types exhibited significant variation from management class distributions of all other sites combined, suggesting variation in distribution among management classes was influenced by ecological differences among habitat types.

Similarly, sex ratios were highly variable. Overall there was a significant male sex bias of 1.22:1 for the entire sample (n = 1804, $p < 0.001$). Only a ravine site (RAV1) showed a significant female bias. *Leucaena* stand habitat displayed the strongest and most consistent trend, with all three replicates showing highly significant male biases.

Hierarchical clustering elucidated similarities among sites in distributions of snakes among management classes (Figure 6). The urban site URB2 (node "A") and ravine forest site RAV3 (node "B") were distinct outliers, likely owing to larger and smaller proportions of mature individuals in samples (Figure 5). Node "C" was comprised of four sites and included two geographically proximate limestone forest sites at the northern end of the island. Node "D" contained six sites with a mix of four habitat types; two scrub forests (SCR1 and SCR3) were clustered closely, and while URB1 and URB3 were under the same node they were in separate subclusters. The remaining node, "E," demonstrated the most apparent clustering by habitat type, including all three *Leucaena* replicates and two remaining savanna sites clustered closely together. Examination of geographic distributions of sites by clustering node (Figure 6) indicated little appreciable pattern in geographic distribution of similarity in management class composition.

Logistic regression revealed site-by-site variation in prevalence of juvenile Brown Treesnakes far outweighed any effect of habitat type (Table 3). The top habitat model for juveniles (*hab*) outperformed the intercept-only model by 3.29 AICc units, indicating some contribution of habitat type, but the site model outperformed the habitat model by 53.47 AICc units, indicating an overwhelming amount of inter-site variability beyond any habitat effect. Both forest-aggregated classifications (*fsu* and *frsu*) performed more poorly than the intercept-only model. Thus, variability within habitat types precludes us from making any predictions about prevalence by habitat type, as can be graphically interpreted from Figure 7a. The top model carried 41.8% of model weights, while the remaining 58.2% of weights went to other models including the *site* term. The second model, carrying 40.4% of the model weights, included season and season∗site interaction terms along with the site term; however, the effect of season was non-significant ($p = 0.677$) and appeared to be included only because of the significant increase in juvenile snakes at the URB2 site during the wet season ($p = 0.006$).

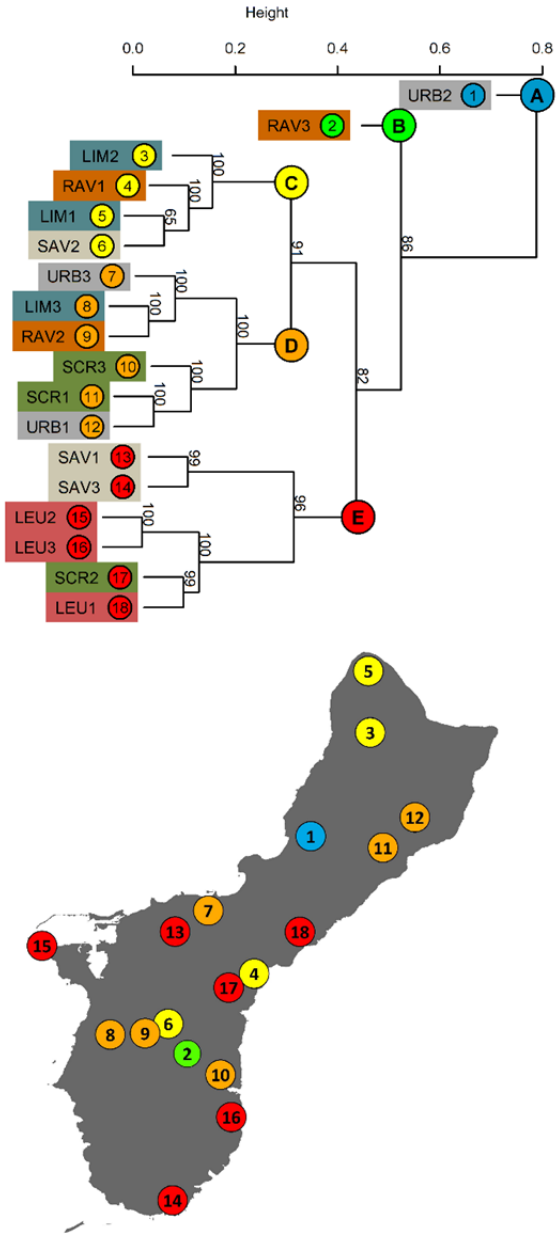

Figure 6. Dendrogram depicting clustering of sites by similarities in distribution of sampled snakes among management classes, with corresponding locations indicated on the map. Values on dendrogram branches (82–100) denote approximately unbiased p-values, with high values (e.g., 95%) strongly supported. "Height" (no units) is a measure of demographic similarity among data points and clusters. LIM = limestone forest, SCR = scrub forest, RAV = ravine forest, LEU = *Leucaena* stand, SAV = savanna, URB = urban.

Table 3. Results for the full logistic regression model set for respective management classes of snakes. Top model ΔAICcs and weights are in bold. K = number of model parameters. Habitat classification schema: *site* = separate term for each of the 18 sites surveyed; *hab* = six habitat classes; *fsu* = three levels, forest, savanna or urban; *frsu* = four levels, forest, ravine, savanna or urban. *seas* = season (wet or dry).

		Juveniles		Mature Males		Mature Females	
Model	K	ΔAICc	Weight	ΔAICc	Weight	ΔAICc	Weight
*site + seas + site*seas*	36	0.07	0.404	24.49	0.000	23.09	0.000
site + seas	19	1.71	0.178	9.41	0.004	7.51	0.009
site	18	**0.00**	**0.418**	10.04	0.003	5.83	0.022
*hab + seas + hab*seas*	12	54.22	0.000	2.81	0.118	12.04	0.001
hab + seas	7	55.23	0.000	2.96	0.109	4.97	0.034
hab	6	53.47	0.000	4.34	0.055	3.15	0.083
*frsu + seas + frsu*seas*	8	56.22	0.000	4.00	0.065	8.49	0.006
frsu + seas	5	61.49	0.000	5.58	0.029	3.76	0.062
frsu	4	59.98	0.000	6.86	0.016	1.89	0.157
*fsu + seas + fsu*seas*	6	56.07	0.000	**0.00**	**0.480**	4.62	0.040
fsu + seas	4	60.89	0.000	3.61	0.079	1.87	0.158
fsu	3	59.44	0.000	4.92	0.041	**0.00**	**0.403**
seas	2	58.24	0.000	18.80	0.000	7.97	0.007
Intercept	1	56.76	0.000	19.59	0.000	6.19	0.018

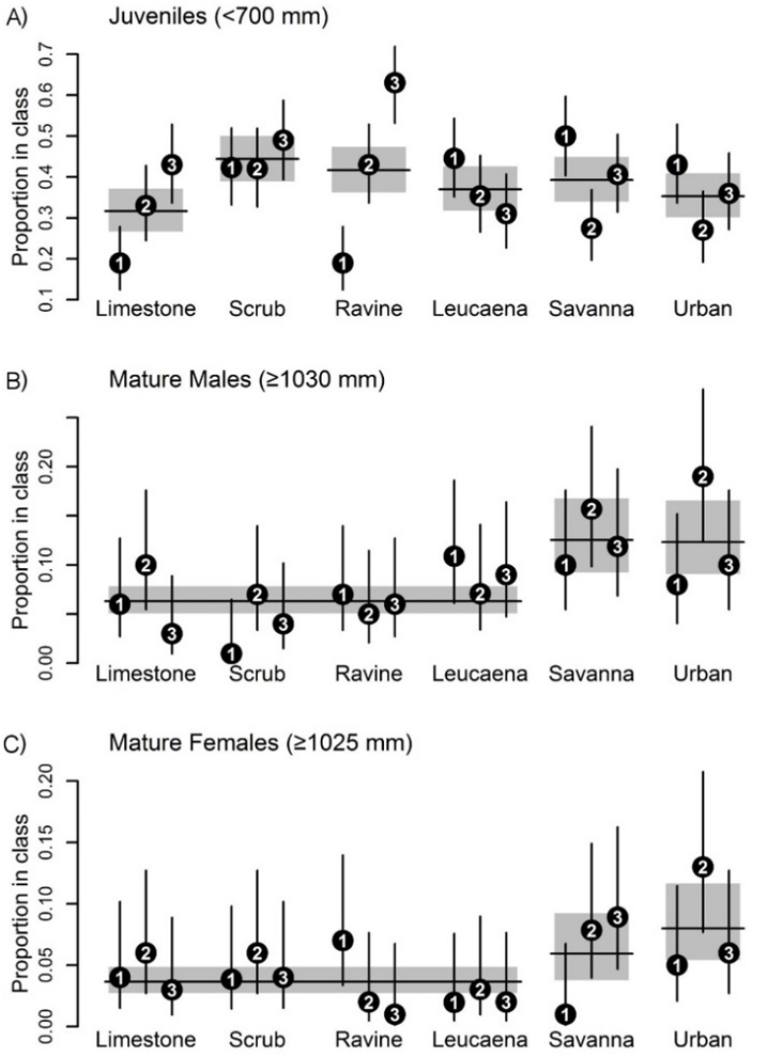

Figure 7. Site estimates for proportions of snakes in respective management classes, with vertical lines representing 95% confidence intervals for the estimate. Numbers in points refer to the replicate number, with locations referenced in Figure 2. Intra-site variability in proportions of juveniles exceeded variation among habitats, but habitat variability (indicated by shaded 95% confidence limit boxes and horizontal mean estimate lines) was still significant when compared to an intercept-only (average) model. Variation in mature males and females was best described by the model that aggregated all forest types into one category.

The top model for mature male snakes (*fsu* + *seas* + *fsu*∗*seas*) indicated significantly higher prevalence in savanna and urban habitats and lower prevalence in forest habitats pooled under a single estimate, suggesting little variability among forest habitat types and not enough intra-habitat variability among replicates to warrant inclusion of a term for each site (i.e., there was more variability among these three habitat types than among replicates within them; Figure 7b). The *fsu* term was included in models carrying 60% of model weights. The next-highest scoring habitat classification was *hab*, with the top habitat model outperforming the intercept-only model by 16.78 AICc units, indicating significant variation by habitat but not enough to warrant breaking four forest types into separate classes. An effect of season was present in models carrying 89% of AICc weights, with model-averaged coefficients indicating a significant increase in prevalence of mature males in samples during the wet season, though interaction terms indicated this was much more pronounced in forest habitats and male prevalence was lower in savanna and urban habitats during the wet season.

Variation in prevalence of mature females in samples was best described by pooling forest habitat types, with the top model containing only the *fsu* term. The among-habitat variation model (*hab*) still outperformed the intercept-only model, but only by 3.04 AICc units. Similar to mature males, the overall forest prevalence of mature females was lower than in savanna and urban habitats (Figure 7c). Models for mature females incorporating a *seas* term carried only 32% of model weights, with the coefficients indicating fewer mature females in the wet season, though the *p*-value for this effect was non-significant.

Discussion

Landscape-scale sampling revealed significant heterogeneity in distributions of snakes among management classes (Figure 5). While variability among replicates within habitat types was considerable (e.g., ravine forest replicates), when samples were pooled by habitat type, each habitat type differed significantly from the reference distribution generated by pooling all other habitats. However, the nature of this variability does not suggest any obvious hypotheses regarding ecological or population processes driving many of these differences, with the exception of larger snakes being found in savanna and urban habitats. Snakes of reproductive size (females greater than > 1025 mm and males > 1030 mm SVL per Savidge et al. 2007) were rare in all samples (Figures 3 and 5), particularly within forest habitats. This relative dearth may be a result of decreased survival or reduced growth rates resulting from scarcity of rodent and bird prey, or a combination thereof. Proportions of mature males and females were relatively consistent among forest habitat types and demonstrably higher in savanna and urban habitats, with highest proportions of mature individuals of both sexes at the URB2 site. Presence of more mature male and female snakes in savanna and urban habitats may be explained by a higher prevalence of large-bodied prey species, namely grassland rodents in savannas and commensal rodents and introduced birds and poultry in urban residential areas (Savidge 1988; Savidge 1991; Siers 2015). The relatively higher proportion of larger snakes in urban habitat may also be partially associated with a higher frequency of road crossings by larger snakes (Siers et al. 2016).

Although Rodda et al. (1999c) reported historical samples had not deviated from a 1:1 sex ratio in any meaningful way, the male-biased sex ratio we observed (1.22:1) was consistent with the observations of Savidge (1991) wherein she found a 1.44:1 male bias in a sample of 897 snakes collected between 1980 and 1987. Our sex bias result, based upon more systematic and finely-stratified sampling, indicates that while there is significant variability among sites within habitat types, some habitat types (scrub forest, *Leucaena* stand, and savanna) do demonstrate a significant sex bias, at least over the one- to two-year span of our sampling efforts. This apparent sex bias may be real (e.g., due to more male hatchlings or higher mortality of females) or perceived (due to higher detectability of male snakes, e.g., Christy et al. 2010). Validation of control tools such as traps and dead neonatal mouse baits in a marked and geographically closed snake population (Tyrell et al. 2009; Lardner et al. 2013) showed no sex biases, so a male-biased population is not likely to influence the effectiveness of these tools. A male-biased population may influence the relative utility of pheromone lures currently in development that attract reproductive male Brown Treesnakes (M.R. Parker, James Madison University, unpublished data). If the apparent male bias in larger snakes is due to an inability to detect larger and potentially gravid female snakes—a segment of the population that is rarely found and about which little is known—this would likely have negative consequences from a management perspective.

Proportions of juveniles were highly variable and unpredictable on the basis of habitat type. Considerable site-by-site variation existed, with predicted proportions ranging from 19% at LIM1 and RAV1 to 72% at RAV3 (Figure 7a). Though proportions within scrub forest and *Leucaena* stand sites were relatively consistent, other habitat types showed more

variability with both extremes of prevalence occurring in ravine forest. These results were strongly supported by relative model weights (Table 3). In exploratory analyses we sought a connection between mature females in good body condition and proportions of juvenile snakes found at a site, hypothesizing that more robust females may be producing more and larger clutches that might explain some of the variability in juvenile relative abundance; however, no such correlation was supported by the data. Gravid female Brown Treesnakes are rarely found on Guam (Savidge et al. 2007; Siers 2015) and little is currently known about their movement or oviposition site selection behaviors.

Effects of season on proportions of juvenile or mature snakes collected were relatively minor and varied among sites and habitats in ways that did not give clear indications of any causality. However, the presence of seasonal effects suggests that a thorough population characterization at a given site should be based upon samples collected in both seasons. Seasonal differences in rainfall may influence breeding behavior (e.g., Brown and Shine 2006), resulting in "pulses" of small snakes; however, our results do not provide strong support for such a hypothesis, and previous work on Brown Treesnake reproductive biology indicates no evidence for seasonal reproduction on Guam (Savidge et al. 2007).

We found little evidence of regional similarities in distributions among management classes (Figure 6). The high degree of variability among replicates within habitats and broad geographic distribution of those replicates did not appear to translate to regional similarities in distributions. This result suggests little spatial autocorrelation in distributions of snakes among management classes, at least at the scale of our sampling, and a greater role for small-scale local factors (i.e., microgeographic variation) in structuring populations.

Our investigation revealed several interesting results for which we have no strong causal hypotheses, such as female bias in ravine habitat, male bias in *Leucaena* habitat, and increased prevalence of mature males in urban habitats during the wet season. In the absence of supporting literature or logical arguments for these differences, we decline to speculate further on mechanisms causing these results. To the extent that such differences may be meaningful from an invasive species management or ecological theory perspective, these results might trigger further research designed to replicate the results and test plausible hypotheses.

As depicted in the habitat classification map in Figure 2, Guam's landscape represents a complex matrix of interspersed fragments of varying habitats, with relatively few large uninterrupted tracts of a single habitat type. Even short-range movements of Brown Treesnakes across this landscape might constitute movement among multiple habitats. Such diffusion likely reduces differences in population characteristics that might emerge among large uninterrupted tracts of very different habitat, and may explain why more drastic differences among habitats were not observed in our sampling.

Our sampling occurred along habitat edges, which has the potential to introduce some bias, either in detection (e.g., larger snakes on the ground—see Siers 2015—may be less detectable due to denser vegetation) or distribution throughout the habitat (e.g., smaller snakes may prefer denser vegetation of edge habitats). Recent work (P. Klug, USGS, unpublished data) indicates some differences in size distributions among snakes sampled from edge versus interior habitat. However, these differences may also be influenced by size-based heterogeneity in detectability and also by observer effects when searchers are forced to navigate through dense vegetation with difficult footing. Additionally, observers can only reliably detect snakes in the open sub-canopy or lower strata of the canopy; data do not exist on size distributions of snakes in higher canopy strata. For these reasons, we are reluctant to say that size distributions from forest interior searches are the "true" distributions for the population as a whole. Given the difficulties of navigating dense tropical forest understories, conducting interior searches would have been logistically impractical and would have added data of limited value. As previously noted, Guam's habitats are highly fragmented and a significant portion of forest habitat is actually edge. Edge habitats are also the typical locations of Brown Treesnake interdiction and resource protection activities (i.e., trap and toxic bait transects surrounding electrical infrastructure and ports).

The management consequences of our results vary depending on the particular stage of the invasion process (Table 1). At the transport stage, juvenile snakes may be of greater risk as evidenced by their prevalence in the sample of interdicted snakes in outbound cargo (Vice and Vice 2004), possibly because they are not attracted to rodent-based control measures protecting cargo ports such as traps (Rodda et al. 2007) and toxic dead neonatal mouse baits (Lardner et al. 2013); the high proportion of juvenile snakes across all habitats on Guam suggests that efforts directed towards intercepting juvenile snakes in transportation areas are critical. At the detection lag stage of an invasion, as might occur if incipient populations are to become established in other snake-free locales such as Hawaii, small

snakes, with lower detectability (Christy et al. 2010), are less likely to be observed, and all snakes are likely to be at low abundance.

Reproductively mature snakes pose high risk in terms of various invasion stages and potential for impacts. Mature females, particularly worrisome if transported, occurred at relatively low frequencies (~ 3.57%) in forest habitats, but at higher frequencies in savanna (~ 5.94%) and urban (~ 7.67%) habitats. The difference in proportions of mature females between forest and savanna was not statistically significant at $\alpha = 0.05$ ($\chi^2 = 2.91$, $p = 0.088$), while the difference between forest and urban habitats was ($\chi^2 = 8.65$, $p = 0.003$). The higher prevalence of larger males and females in urban habitats, if replicated within a new incipient population, may increase likelihood of reporting by humans. Spread of an incipient snake population may be accelerated by mature males and females due to their reproductive potential and higher probability of crossing roads and other habitat gaps (Siers et al. 2016). The impact risks associated with Brown Treesnakes are likely to increase with snake size, as larger snakes take a wider range of prey species (Savidge 1988; Shine 1991; Siers 2015), leading to potential extirpation or extinction of native prey as documented on Guam by Savidge (1987). Due to their ability to inflict more serious bites and ingest larger prey items, larger snakes also pose greater threat to humans and domestic animals. While our results may suggest that these impacts would fall more heavily upon savanna and urban habitats than on forest habitats, it should be noted that Brown Treesnakes on Guam have already effectively extirpated forest fauna, causing a shift to a smaller proportion of mature snakes (Savidge 1991; Siers 2015). This is not likely to be the case in a novel environment with plentiful forest prey.

Recent successes with experimental trials involving aerial application of toxic baits suggest landscape-level suppression of BTS on Guam could be achievable; a majority of snakes will take aerially-distributed baits suspended in the canopy (Dorr et al. 2016) and an automated system for the manufacture and aerial delivery of baits has been developed and evaluated (S. Siers, USDA, unpublished data). Based on what is known of size biases associated with use of dead mouse baits (Lardner et al. 2013), preliminary modeling exercises predicting the effects of aerial baiting campaigns for Brown Treesnake suppression indicate that demographic variation among sites at the outset of treatments may influence the level of effort necessary to achieve suppression objectives (B. Lardner, Colorado State University/US Geological Survey, personal communication).

High and highly variable prevalence of snakes too small to be effectively targeted by current control technologies likely poses the single greatest threat to prospects for successful landscape-scale suppression or localized eradication of Brown Treesnakes. This variability does not appear to be predictable based on currently available data. While adult snakes are relatively easy to target with traps or toxicant baits, failure to completely control adult females may defeat suppression objectives by allowing production of new juvenile snakes too small to be effectively targeted.

Much of the uncertainty in effective landscape-scale control lies within the transitional class of snakes. Theoretically, as smaller snakes mature, they become susceptible to rodent baits (Rodda et al. 2007; Lardner et al. 2013) prior to becoming reproductively mature (Savidge et al. 2007) (see the transitional stage in Figure 4). This stage of development may offer a "window for control" during which snakes are susceptible to control but not yet reproductive. Repeated applications of trapping or toxicant delivery may target maturing snakes, potentially killing many snakes before they can reproduce. However, uncertainty remains with regard to the relative timing of transition to targetability and on to maturation.

Though it has yet to be demonstrated that native species reintroductions would be successful with local suppression or elimination of Brown Treesnakes, nor have the thresholds below which snake numbers must be suppressed been evaluated, it is recognized that this is a necessary prerequisite to species recovery on Guam (Brown Treesnake Technical Working Group Strategic Plan, unpublished draft). The strong persistence of Micronesian Starling (*Aplonis opaca*) populations within urban/residential habitat on Andersen Air Force Base (AAFB), Guam —where Brown Treesnake populations have been consistently suppressed through trapping—suggests potential for successful bird reintroductions or the expansion of this starling population into neighboring forest habitats upon sufficient suppression. Reintroductions of flightless Guam Rails (*Galliallus owstoni*)—extinct in the wild—into large snake-proof enclosures within which snake abundances have been drastically reduced or eliminated, such as the Habitat Management Unit on AAFB, is seen as a logical first step in native species recovery (AAFB and Guam Division of Aquatic and Wildlife Resources, personal communications).

In this manuscript we offer a framework for evaluating how ontogenetic shifts in management risk by sex and size class, invasion stage, and variability of distributions among management classes within and among habitat types can influence management considerations. While some habitat

trends are significant and consistent, the overall result is one of much heterogeneity and little predictive ability. Any simulation modeling of candidate suppression scenarios must incorporate the full range of variability documented here.

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